IX. *On the Growth and Composition of the Ovarium of* Siphonodon celastrineus, *Griffith, especially with reference to the subject of its Placentation. By* Joseph Dalton Hooker, *Esq., M.D., F.R.S. & L.S.* (With a Plate, Tab. XXVI.)

Read June 16th, 1857.

In a learned memoir upon some remarkable plants in the Hon. E.I.C.'s Botanic Gardens, Calcutta*, Mr. Griffith established the genus *Siphonodon* upon a very curious Malacca tree of doubtful affinity and singular structure, and accompanied his description with many observations of the highest interest and importance to the student of structural and morphological botany. Amongst these observations is one, which, though published for now nearly fifteen years, has never attracted the attention of botanists, owing to the limited circulation of the Calcutta Journal, but which, from its bearing on the subject of placentation, has a peculiar interest to myself; for it appears to me to be, if correct, the strongest proof hitherto adduced in favour of the theory which regards the placenta as terminating the axis, and not as being referable to the carpellary leaf. To this theory my own experience is opposed, and as I believed I had proofs of the invalidity of what appeared to me to be the most cogent arguments previously adduced in favour of it, I more particularly wished for an opportunity of testing the accuracy of Griffith's statement with regard to *Siphonodon*. Mr. Griffith's conclusion is, "I beg to propose this plant to botanists, as an instance in which the placenta is the termination of the axis, bearing around its base a verticillus of ovula, and produced upwards into a stigma, a single organ, surrounded for the most part by a style with which it has no connexion." (*loc. cit.* p. 255.)

The foundation for this proposition is Griffith's conviction that the ovules, of which there are many in one horizontal series, are developed on an axis in the centre of the flower, independently of the carpellary leaves, and not enclosed by them or by any other organs except the perianth; and that the subsequently developed carpellary leaves form a verticillus externally to the ovules, and rising upwards and inwards, finally enclose them. These conclusions appear to me to be founded on erroneous observations, and the chief object of the present communication is to lay before the Society my reasons for supposing them to be so.

I am indebted to my friend Dr. Thomson, who was well-aware of the interest attached to this plant, for specimens of *Siphonodon* flowers preserved in spirits, gathered from the same tree, I believe, in the Hon. E.I.C.'s Botanic Gardens, which was described by Griffith. These flowers are in all stages of growth, from buds scarcely perceptible to the naked eye, to fully expanded flowers, which measure about $\frac{1}{3}$ inch in diameter: I find, however (as is usual in flower-buds), that there is little relation between the size of the bud and the development of its reproductive organs. In all, I invariably find both whorls of the perianth to be fully formed in two closely imbricated series, before any traces of the

* Calcutta Journal of Natural History, vol. iv. no. xiv. July 1843, p. 231, t. 14.

ovules or carpellary organs are differentiated, and I shall therefore commence with the bud at this stage, as the first in which the structure and composition of the ovary can be studied.

1. In the first stage (Pl. XXVI. fig. 2) the bud is a minute turbinate body, about $\frac{1}{4}$ line in diameter, with little external distinction between the flower and peduncle. On a vertical section (fig. 3), the double perianth is found to be wholly superior, the sepals placed highest, then the petals, then the stamens, whose anthers (*s*) form minute clavate bodies, sessile at the very base of the petals. All these organs are placed considerably above the plane of the centre of the flower, which presents a depressed area with a very low broad central mamilla, whose vertex scarcely rises to the level of the plane of the base of the stamina. At this period the ovary is manifestly plunged into the apex of the peduncle, and can by no means be regarded as invested by the true calyx, the bases of the sepals being obviously inserted in the margin of the broad obconic apex of the peduncle. In some buds at this period, the central mamilla of the axis (the future style of Griffith) is surrounded by a low broad ridge, or annulus, correctly described by Griffith as belonging to the carpellary leaves.

This is Griffith's earliest stage; he, however, regards the central mamilla as the pistillum itself, a view which is irreconcileable with the fact that the ovarian cells are in the next stage developed below the plane passing through its base, and removed from the circumference of its base.

2. The next marked stage (fig. 4) is that in which the anthers are fully formed and their polliniferous cavities defined, and hence well distinguishable. At this period the central mamilla has risen, and presents the appearance of a style consisting of a short column with a depressed conical hemispherical base; it is more or less invested by the annulus (*a*), which was obscurely seen in the first stage; this annulus has five notches at its mouth, is very thick, and points upwards and inwards towards the apex of the column, being usually applied to its base. The relative position of the stamens and perianth to the plane of the ovarium is the same as in the first stage; vascular bundles are developed in the petals, and are traceable continuously downwards into the peduncle, and branches from these bundles supply the stamens also. The stamens arch over the annulus, and the conniving apices of the anthers almost reach the central column; they are opposite the five notches in the annulus, and five slight ridges on the annulus correspond with its teeth and with the interstices between the anthers.

At this period the ovules are first developed. A whorl of about twenty minute cavities are traceable in a plane below the point of junction of the annulus and conico-hemispherical base of the column; the ovarian cavities (*o*) point downwards and outwards. The ovules appear as minute papillæ, occupying the base of each cavity towards the axis; they present no distinction of parts whatsoever. No vascular bundles are discernible in the ovarium.

In this stage I have included the second and third stages of growth described by Griffith, because, after examining an extensive series of buds, I find very great irregularities in the time of appearance of the ovarian cavities, relatively to the development of the annulus. In some buds I find the ovules formed before the annulus has reached

the rounded shoulders of the column, in others not till after it has enveloped that organ. It is at this period, however, that the important difference between my observations and Mr. Griffith's occurs, and as it is upon this that the whole question of the placentation turns, I have taken every means of endeavouring to arrive at the truth. Griffith says, that at the period when the base of the central column becomes concealed by the growth of the annulus, very young ovula may be detected, apparently attached around the whole base of the column, and not presenting any manifest relations with the carpellary leaves. He adds, that at this time a double long section had not shown him any solution of continuity resulting from forcibly pulling back the carpellary leaves (annulus) and thus exposing the ovula. On the other hand, I, at no period, find the ovules to be developed freely at the base of the column; I have sought in vain between the annulus and column for any such appearance, removing the annulus piecemeal with the utmost caution; and in every double vertical section that I have made, I have found the ovarian cavities to be developed even at a much earlier period than that indicated by Griffith, below the junction of the annulus and column, manifestly within the substance of the ovary. The cavities containing the ovules cannot at any period be exposed without tearing the annulus, which, however, owing to the delicacy of the tissues and the excessive minuteness of the organs, it is sometimes difficult to avoid doing.

3. In the succeeding stage (fig. 5), the anthers are fully formed, and, arching inwards, conceal the whole vertex of the ovary, leaving the apex of the column alone exposed between their apices (fig. 8). The cylindrical portion of the column has lengthened, and is terminated by a capitate stigma-like head; its conical base is proportionally smaller and more depressed. The annulus is very much thickened and grown in all dimensions; it has advanced up the column, and presents on a double vertical section two broad shoulders embracing the column, which it thus sheaths in a tube; its upper surface is moulded by the pressure of the anthers which lie between the five radiating ridges accurately described by Griffith. The five teeth (figs. 8 *t* & 6 *t*) terminating the ridges are now more prominent, turn upwards, and are very cellular and fimbriated; and a distinct groove is formed on the surface of the annulus, close to its orifice and concentric with it. The ovarian cavities are fully formed, linear-oblong, and all point outwards, but some upwards and some downwards. The ovules are horizontal with an obscure lateral raphe, and each is conformable to its cell. The column has an evident cuticle, as has also the contiguous wall of the annulus. At this period vascular bundles appear in the ovary, and are traceable downwards from each ovular insertion, and transparent lines are continued from each ovule upwards into the annulus, to whose inner face these ascending lines are parallel and contiguous. The tissues of the sheath of the annulus are pale and translucent. Mr. Griffith says, that at this period the stigmatic surfaces will be found at the conical base of the central column, at the point of its junction with the base of the annulus; he says, "the lines of communication, by which each isolated ovulum is placed in the usual conditions to receive the male influence, will be found to terminate on the circumference of the conical base of the central column." On the contrary, I find the cuticle to be uniformly extended over the points indicated; but its tissue is there rather looser, the cells which form it being elongated inwards, giving when torn the appearance of stigmatic

tissue, and causing that fragility of that part of the ovarium which led to Griffith's supposing that the ovarian cells were formed subsequently to the freely developed ovules. The true stigmatic canals I find terminating in the papillose fimbriated teeth of the annulus.

4. Towards the period of expansion of the flower (fig. 6), a considerable change is found to have taken place in the relative proportions and positions of the ovary and perianth. Owing to the upward direction of the development of the ovary, it is now half-superior, in the usual acceptation of that term. The *stamens* (fig. 9) form a closely imbricating whorl, appressed to the surface of the annulus, the stigma-like head of the central column appearing in the space between their apices, and the five cellular fringed teeth of the annulus also projecting.

On removing the stamina, the protuberant surface of the annulus is more strongly 5-ridged, and the groove round its orifice is deeper. A double vertical section shows that the column is much elongated, and its surface covered with a more evident cuticle, as are its capitate stigma-like apex and the adjacent walls of the annulus. The external surface of the annulus is also covered with a similar cuticle, except at the groove surrounding its orifice, and on the fimbriated teeth, which are manifestly the true stigmata, and are formed of loose papillose tissue (fig. 13). The ovarian cavities are at this period found to be considerably displaced, some being carried a little upwards and others downwards, so that two or three are often exposed at one vertical cut. Unrollable spiral vessels are now found in the vascular cord that passes downwards from the ovules, but none in the transparent line that passes upwards from the ovules parallel to the inner walls of the annulus, these lines being formed of loose conducting tissue, terminating in the stigmatic teeth at the orifice of the annulus. A transverse section of the annulus (fig. 10) now shows five pale spots of loose cellular tissue; these are the stigmatic canals, placed very close to the inner walls of the annulus.

5. At the period of expansion (fig. 7) the stamens are found to have risen from the surface of the annulus, and the stigmatic teeth are sphacelated and covered with pollen-grains, which adhere to its surface and to the surface of the mouth of the tube; but I have not succeeded in tracing the pollen-tubes into the stigmatic canals, probably owing to the excessive minuteness of the pollen in this plant.

The differences between my own and Mr. Griffith's observations are, first, in the ovules being developed in cavities of the ovarium, and not free at the base of the conical central body, which he has mistaken for a placental development; secondly, in the presence of a cuticle over the whole surface of the said body and on the contiguous walls of the annulus; thirdly, in the absence of any vascular bundles passing from the ovules upwards into the annulus; and fourthly, in the absence of any stigmatic puncta at the base of the central column, and of stigmatic lines passing from these inwards to the ovules. The groove round the mouth of the annulus, the absence of cuticle over it, and the structure and consequently the stigmatic nature of the teeth of the annulus, seem further to have escaped Mr. Griffith's notice.

If my observations are correct, the composition of this very remarkable ovarium is reducible to the known modifications of carpellary structure, and may be regarded as consisting of a whorl of five connate carpels adnate to a central fleshy axis or torus;

this torus being produced, as in *Nymphæa*, *Victoria*, &c., into a styliform and stigma-like body. Each carpel bears two ovules on each of the ten marginal placentæ, making twenty ovules in all. The annulus is the free upper portion of the five confluent carpellary leaves; the five ridges are the lines of junction of these; the five stigmata are each double, formed by the terminations of the confluent placental margins of the adjacent carpels, as in *Papaveraceæ* and many other Orders.

There is one point, however, to which further allusion is necessary, as possibly in part explaining Mr. Griffith's views; and this is, the above-mentioned line of loose cellular tissue that extends from the base of the central column to the ovarian cavities, and which is met at the ovarian cavity by the true stigmatic tissue. It is very possible that this line indicates the existence of a stage in the early state of the ovarium in which the carpellary leaves were not completely closed; for though I feel satisfied that the ovules of this plant are at no period independent of the carpellary leaves, and are indeed formed in cavities of those leaves and from their margins, it does not follow that there may not have been a free opening to these cavities, or one closed only by a very lax tissue. It is indeed held by some botanists, that all carpellary leaves are congenitally open, and close more or less completely afterwards; an opinion which is not as yet absolutely proven, though I cannot but think that the open ovary of *Coniferæ** and its allies is a strong argument in its favour. This however, if true, by no means reconciles Mr. Griffith's observations, or his theoretical view of the structure of the ovary of *Siphonodon*, with my own.

The structure I have described in *Siphonodon* suggests a different view of the affinities of this obscure genus than those which have been doubtfully adopted by Griffith, though in the absence of ripe seeds it will be difficult to establish these, and I shall not therefore attempt to do so now.

In submitting this very singular plant, then, as a strong proof of the validity of those laws of carpellary placentation which it has been supposed to have subverted, I cannot refrain from expressing my admiration of the learning which Mr. Griffith has displayed in his discussion of the view he somewhat hastily adopted;—of the guarded manner in which he expresses his opinion;—of the full weight he gives to every structural point that seems to him to militate against it, and of the candour with which he states every adverse argument that suggests itself to him. Though I believe his observations and conclusions to be erroneous, it must be recollected that the plant is a very anomalous one, its parts exceedingly small, and that my experience assures me that specimens preserved in spirits, such as I examined, are in many respects much better for determining structural points from than living ones are. Mr. Griffith's paper further abounds in acute observations on many other points in the structure of *Siphonodon*, to which I have not alluded; and it contains, in a note, a short abstract of the only accurate account hitherto published, so far as I know, of the development and true nature of the ascidia of *Nepenthes*†.

* It appears more consonant with the known laws of vegetable morphology to regard the Coniferous ovary as an arrest of the usual tendency of ovaries to close, than to suppose the ovaries of most Phænogams to be congenitally closed, and that of Conifers open.

† Some years ago I prepared drawings of the development of the pitchers of *Nepenthes*, from plants in the Royal Garden at Kew. These confirm Griffith's observations in every particular, and prove the pitchers to be modifications of excurrent midribs. Each pitcher commences as a gland at the anterior apex of the conical mamilla, which represents

Before dismissing the subject of carpellary placentation, I would state that the other arguments in favour of free axile placentation, to which I have alluded at the beginning of this communication, are, the free central placenta of *Primula*, and the position of the ovule of *Taxus*. I am not aware of any deviation from the free central placentation having been observed in *Primulaceæ* except by Prof. Henslow, who kindly placed in my hands for examination a monstrous flower of *Primula vulgaris*, in which two ovaria presented ovules developed on the confluent margins of some of the carpellary leaves, far removed from the base of the ovary, and wholly unconnected with the central placenta, which still existed, but in a reduced form, and bore ovules.

The other case is that of *Taxus*, adduced I believe originally by M. Schleiden, who considers the ovule as terminating the bracteate peduncle or rachis which bears it. That this view is not tenable appears to me to be proved by the fact that I have found two and even three ovules at the apparent apex of the peduncle. I further cannot but consider the bracteate peduncle of the female flower of *Taxus** as a genuine cone, the majority of the bracteæ of which bear no ovarian scale and ovule. When more than two ovules are developed in this cone, these almost invariably wither and disappear at a very early period; but I have examined partially diseased cones of *Taxus*, in which the second ovule had enlarged and persisted in a scale below the terminal one.

With such a preponderating mass of evidence in favour of carpellary placentation, derived from the normal condition of both simple and compound pistilla, in which the relation of the parts cannot be misinterpreted, and from monstrous states of ovaries whose composition is more obscure, it does seem to me unphilosophical to call for the operation of a second law to explain the comparatively few exceptional examples of placentation that are not at once referable to the carpellary. Of these exceptional cases, *Primulaceæ*, *Caryophylleæ*, and their immediate allies have always been supposed to be the most difficult to explain away, but *Caryophylleæ*, both in their normal state and as monsters, present many cases of carpellary placentation, and Professor Henslow's *Primula* demands a double law for one flower, if the free axile placentation be not considered a modification of the carpellary.

If it be admitted that the floral whorls are formed from leaves, even when appearances

a leaf in the earliest stage of its development. A contraction below the gland separates it from the lamina of the leaf, which is independently developed with a convolute vernation.

While upon this subject, I may further mention, that the bilobed lamina of *Dionæa* is unquestionably the true lamina of the leaf of that plant; and that it is inflexed in early vernation, as in *Drosera*, to which it is so closely allied, and to which it is further united by means of *Aldrovandra*.

Of *Aldrovandra* I may remark, that this very rare and singular plant has been rediscovered by Dr. Thomson in the immediate vicinity of Calcutta. It was originally found there by Dr. Roxburgh, but unsuccessfully sought for by Dr. Wallich, Griffith, Voigt, and indeed every Calcutta botanist. Though unknown in any intermediate spot between Europe and Calcutta, I can find no difference whatsoever amongst the specimens from these widely-sundered localities.

* The fleshy cup of *Taxus*, which is usually called a disk in botanical works, but which is regarded as an arillus by Schleiden, is undoubtedly the outer coat (primine) of the ovule; it is developed at an early stage as an annulus in immediate contiguity with the second coat (secundine): this second coat in *Taxus*, as in many other Conifers, becomes the outermost covering of the seed, or tegmen. I have ventured to allude to this here, as I am not aware that the true nature of the integuments of the seed and ovule of *Coniferæ* has been correctly stated in any general systematic work.

are against this view, and when it may be impossible to demonstrate it; and that this law allows of no exception,—it seems natural to suppose that the law of the formation of ovules in one of these whorls should be regarded as no less absolute, and that any explanation that does no violence to nature should be accepted to account for apparent exceptions, in preference to abandoning the general law and adopting a particular one for those exceptions. Under this point of view I should prefer agreeing with those botanists who consider that all placentation is axial, and that carpellary insertion is to be explained by supposing axes to be produced upon the carpellary leaves, rather than conclude that nature resorts to two totally distinct and opposite principles in effecting the same purpose with the same organs. The instances, however, of the ovules being normally developed on the margin of the carpels, are so extremely numerous and convincing, and the cases of insertion which are not at once reducible to this relation of parts are so few and so scattered through different Natural Orders, that I cannot but regard the latter as insufficient to invalidate the law in question, and to demand the operation of another.

EXPLANATION OF THE PLATE.

Tab. XXVI.

Fig. 1. Flowering branch of *Siphonodon celastrineus*:—of the natural size, from Mr. Griffith's drawing.
Fig. 2. Bud at the earliest period of the appearance of the parts described:—of the natural size.
Fig. 3. Vertical section of ditto; *s.* stamens.
Fig. 4. Vertical section of upper portion of more advanced bud, the ovular cavities having just appeared.
Fig. 5. Another bud further advanced, the stigmata formed, and vascular cords to the ovules.
Fig. 6. Flower about to expand, cut vertically. The ovules are displaced, and the annulus swollen.
Fig. 7. Flower after impregnation, with the stamens still attached.
Fig. 8. Annulus from fig. 5, seen from above; *t.* the stigmatic teeth.
Fig. 9. Stamens seen from above, concealing the annulus.
Fig. 10. Transverse section of annulus, showing the five stigmatic cords or passages.
Fig. 11. Portion of ditto much more highly magnified.
Fig. 12. Portion of annulus, with stigma, conducting tissue, ovules, and vascular cords.
Fig. 13. Portion of another annulus with stigmata, an ovule and its vascular cord.
All but figs. 1 & 2 more or less highly magnified.